

Brachiopoda

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A phylum of predominantly sessile, filter-feeding marine invertebrates, with a ciliated, tentaculate feeding organ or lophophore and a bivalved shell. The two main living types (with either articulated or inarticulated valves) first appeared in the Lower Cambrian. Articulated forms give the phylum its common name: 'lamp shells'. In recent molecular analyses, brachiopods and phoronids form a single clade.

Body Plan

Within a body plan common to all living brachiopods and phoronids, several distinct types can be recognized (Figures 1 and 2) with differing combinations of character-states (a) shell present, or absent, (b) shell valves connected at a mineralized hinge, or not hinged, (c) mineral component of the composite, organic polymer–mineral shell calcite (calcium carbonate), or apatite (calcium phosphate) and (d) shell cemented directly to the substrate, or attached via a pedicle. The evolutionary lineages that survive at the present day (see Figures 6 and 7) make up two main clades which diverged in or before the Early Cambrian: the rhynchonelliforms (rhynchonellides, terebratulides, terebratulides and thecideidines), whose valves join at a mineralized hinge, i.e. are 'articulated', and the linguliforms (craniates, lingulates and phoronates), whose valves are joined only by soft tissues, i.e. are 'inarticulated', or which secrete a tube rather than a shell. Phoronates (phoronids) are here included among brachiopods on the basis of recent molecular phylogenetic results.

The brachiopod body plan differs radically from that of the more familiar bivalve clams (Mollusca: Pelecypoda). In clams, the shell valves originate on left and right ectodermal mantle folds, either side of the embryonic anterior–posterior (A–P) long axis, and join at a dorsal hinge so that the A–P axis runs between the valves, parallel to the hinge. In brachiopods, by contrast, the A–P axis runs across the middle of both valves and is perpendicular to the hinge region. This initially perplexing layout is explained by origination of the valves at anterior and posterior ends of the embryonic dorsal mantle, later coming to lie opposite one another through a dorsoventral fold (or an equivalent mantle reversal) across the middle of the embryo as it metamorphoses at (or in some cases before) settlement, placing the embryonic ventral side inside the shell, facing the mantle cavity. This 'brachiopod fold' can be interpreted as a corollary of the sessile lifestyle. Phoronids form a chitinous tube instead of a shell, and the (hypothetically) equivalent ontogenetic fold is oppositely directed, placing the embryo's ventral side outermost. It is not clear whether shell mineralization was lost

or was never present in the phoronid lineage (see Figure 7). **See also:** Mollusca (Molluscs)

Fine, chitinous bristles (setae or chaetae) emerge from the larval epithelial surface of all except thecideidine larvae, and from the marginal mantle grooves of the majority of adult brachiopods. These setae sense local conditions and protect the feeding gape. In burrowing linguloids the setae play an important role in directing the movement of sediment grains. Chitinous setae with very similar ultrastructure and mode of formation also occur in some other lophotrochozoans (e.g. annelids).

The ontogenetically anterior–dorsal valve of brachiopods (sometimes termed 'dorsal'), is better known by its traditional name, 'brachial valve', which reflects the support it generally gives to the left and right 'arms' (or brachia) of the lophophore. Similarly, the ontogenetically posterior–dorsal valve (sometimes termed 'ventral') is also better known by its old name, 'pedicle valve', because it often surrounds or partly houses this stalk (where present). The common name for brachiopods, 'lamp-shell', derives from a fancied similarity of the rhynchonelliform pedicle valve to a pottery oil-lamp with its wick in the pedicle aperture. Newly settled brachiopods attach more-or-less permanently to a mineral substrate by means of fine rootlets (many rhynchonelliforms) or cement at the end of the pedicle (lingulates), or by cementing the pedicle valve directly to the substrate (craniates and thecideidines). The smallest living adult brachiopods are *c.* 1 mm long; the largest *c.* 100 mm, but 10–30 mm is more typical. Some fossil forms grew much larger. Lifespan may be *c.* 3–30 years or more.

The two main clades of living brachiopods differ in the way the paired shell valves operate. In the articulated rhynchonelliforms, opposed muscle pairs inserted on the valves create lever arms around the tooth-and-socket hinge, and thus open the valves for feeding, or shut them for protection. Other muscles serve to adjust the position of the shell relative to the pedicle (where present). These are the limits of rhynchonelliform activity. In inarticulated linguliforms, where there is no hinge and the shell valves are joined only by muscles, they are opened by indirect muscle action, working through coelomic fluid pressure, and closed by direct muscle action. Where the pedicle valve

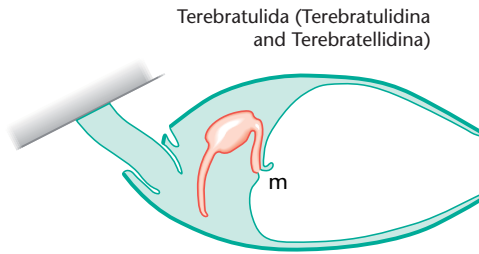
Introductory article

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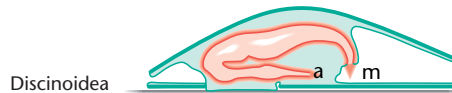
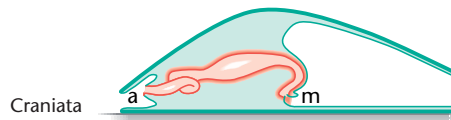
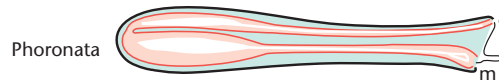
Rhynchonelliform (articulated) brachiopods



Thecideida

(not illustrated)

Inarticulate brachiopods and phoronids



Linguloidea

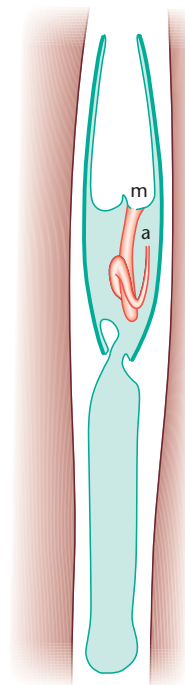


Figure 1 Comparison of the body plans of the principal lineages of living brachiopods. Mouth (m) and anus (a) are marked. (After Nielsen, 1995.) (Not to scale)

is cemented to the substrate (craniates and some discinoids) the feeding gape is closed by muscles that pull the brachial valve into close contact with the substrate. Linguloids burrow by the action of muscles that rotate one valve against the other in a scissors-like action that enables the setae to brush sediment particles backwards. Such burrowing is the most active behaviour of extant brachiopods; it has persisted since the Early Cambrian, leading to the common misdescription of linguloids (e.g. *Lingula*) as a 'living fossil'. It is a surprisingly complex behaviour: in an aquarium, exposed animals have been observed to use their muscular pedicle to arch themselves until the shell gape

points downwards and to work for several hours to reform and reenter a U-shaped burrow.

In all extant brachiopods much of the space between the valves forms a mantle cavity, containing the bilaterally symmetrical lophophore; only a small portion of the space is occupied by body organs. Ciliated tracts line the lophophore tentacles and arms, which adopt various lineage- and growth stage-specific folds and coils. The laminar-flow feeding current passes through the lophophore where food particles (mostly phytoplankton) are captured (**Figures 3–5**). Particles are moved by ciliary currents along the lophophore arms to a central, slit-like mouth, through

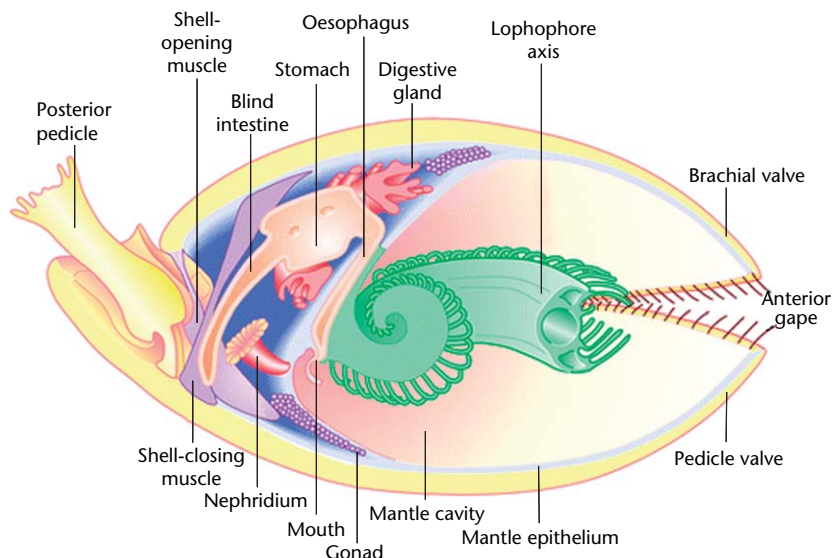


Figure 2 The principal organs of a generalized rhynchonelliform brachiopod. (After Williams and Rowell, 1965.)

which they enter a muscular pharynx, a short oesophagus, a distended stomach and a hind gut. Digestion is partly intracellular, within a digestive gland that opens off the stomach. In rhynchonelliforms there is no anus; waste solids are voided through the mouth. In lingulates, the gut recurves to a right-sided anus that opens into the mantle cavity. In craniates the anus is median, and does not open into the mantle cavity.

Brachiopods have no head, but a nerve cord with ganglia circles the oesophagus and nerves radiate widely. In addition to setae, some developmental stages have statocysts and eyespots. The circulatory system is not well known but, where studied, is open, with one or more contractile 'hearts'. Coelomic canals extend along the lophophore arms and into the epithelium that lines the mantle cavity, where gonads develop from coelomic epithelium. Germ cells escape through paired metanephridia that open into the mantle cavity (**Figure 2**). Sexes are generally separate, though some brachiopods may be hermaphrodites. Fertilization is external, and some or all of the fertilized eggs may be brooded for a while, either in the lophophore or in a special brood chamber. Lingulate embryos develop into long-lived, planktotrophic juveniles with a rudimentary shell, and have high dispersal potential, but rhynchonelliform larvae are lecithotrophic, and generally settle and metamorphose quickly, without feeding. Their dispersal potential is, therefore, generally low. However, some Antarctic rhynchonelliform larvae may spend months in the plankton.

The brachiopod shell and its superficial periostracum are formed by cells of the mantle epithelium at the commissure where the valves meet, and it is continuously remodelled (especially the lophophore support or 'loop' of terebratulids) as the animal grows. Both the periostracum and shell

are complex, layered structures that show important differences in ultrastructure and composition both between lineages, and between pre and postsettlement developmental stages. The primary (sub-periostracal) shell layer is typically granular, the secondary and tertiary (inner) layers, where present, fibrous, laminar or prismatic. In craniates, the proteinaceous periostracum is underlain by laminae of protein-associated calcite (crystalline calcium carbonate), whereas in lingulates (e.g. *Lingula*, *Glottidia* and *Disciniscia*), a chitinous periostracum is underlain by an organic matrix hardened by granules of apatite (calcium phosphate). In embryonic discinoids (e.g. *Disciniscia*), minute siliceous tablets are embedded in the embryonic shell surface; a rare use of silica by triploblastic metazoans. In many brachiopods (craniates and most rhynchonelliforms but not lingulates) the shell is almost penetrated by closely spaced pores (caecae) lined by mantle epithelium. These may be storage organs: when nutrients are plentiful the caecal epithelium may contain up to half the total organic matter, but their evolutionary origins and functions remain somewhat mysterious and they are absent from some extant lineages. Various fossils that may have been stem group brachiopods (e.g. *Mickwitzia*, *Micrina*) are more or less covered with tubular shell pores that appear to have housed setae, while polyplacophoran mollusc (chiton) shells contain pores (called aesthetes) analogous to brachiopod caecae. In some rhynchonelliforms calcitic spicules may reinforce the mantle and lophophore soft tissues.

Structure, development and function of the pedicle varies. In craniates and thecideidines, there is no pedicle and the pedicle valve or its periostracum is cemented directly to the substrate. In some discinoids a short pedicle emerges from a notch in the valve (**Figure 1**) and is cemented to the substrate. In most rhynchonelliforms the end of the pedicle

forms a holdfast, which is cemented to the substrate. The rhynchonelliform pedicle may be short and rigid or long and flexible, and the shell can often be rotated around it. The pedicle may be lost in some rhynchonelliforms that become free lying after outgrowing a small initial anchor. The pedicle reaches its greatest development in linguloids which, uniquely among brachiopods, burrow into soft sediments. The linguloid pedicle is a protrusible, muscular organ (supposedly edible), used for burrowing, shell orientation and rapid retraction.

Habitats, Diversity and Abundance

Brachiopods are strictly marine. They predominantly occupy low energy, often cryptic, habitats such as rocky overhangs below the level of wave action, crevices in reefs, submarine caves, the steeper slopes of the continental shelf, or abyssal deep waters. A few articulates (e.g. *Notosaria* and *Calloria* in New Zealand, *Terebratalia* on the Pacific coast of North America, *Kraussina* on the South African coast) may be found in more energetic locations (e.g. attached to kelp holdfasts) or even in very sheltered sites in the low inter-tidal zone (e.g. under rocks). The pedicles of most rhynchonelliforms attach to mollusc or (very often) other brachiopod shells, as well as to seaweed, rock, gravel, or even coarse sand. The smallest living brachiopod (*Gwynia*) lives interstitially, in gravel. The least typical brachiopod habitat is occupied by

the extant linguloids *Glottidia* and *Lingula*, which burrow in soft sediments, as their ancestors have done since the Early Cambrian. **See also:** Marine communities

Although most biologists have never seen a living brachiopod, they are actually widely distributed and may be locally quite common (Figures 4 and 5). Over 100 genera, mostly rhynchonelliforms, have been recognized among the living fauna while about 5000 fossil genera have been described. As expected for animals with nonfeeding larvae that settle rapidly, rhynchonelliforms show considerable geographic differentiation, with distinctive constellations of endemic genera in marine provinces such as Antarctica,



Figure 4 A group of the rhynchonelliform, articulate brachiopod *Megathiris detruncata* on the wall of a small cave, south coast of Madeira, depth c. 10 m. The largest shell is c. 10 mm wide. There are no setae. (Photo credit: Peter Wirtz.)



Figure 3 Close-up view of the rhynchonelliform, articulate brachiopod *Liothyrella neozelanica* in feeding position with its gape fully open, showing a conspicuous fringe of marginal setae and the curtain-like lophophore forming inhalant and exhalant compartments within the mantle cavity. The inhalant current enters at the sides and the exhalant current leaves centrally. In many fossil and extant deep-water forms, the inhalant and exhalant currents are offset by a median fold or groove in the shell, presumably to minimize recirculation of filtered water. This animal's shell is about 40 mm across. (From a photograph provided by L. Shackleton, Wellington, New Zealand.)



Figure 5 A group of the thecideidine, articulate brachiopod *Pajaudina atlantica* on the roof of a small cave, La Palma, Canary Islands, depth c. 15 m. The complexly folded lophophore is supported by bas-relief ridges on the brachial valve and the shell gapes very widely. Each shell is c. 5 mm wide. As in *Megathiris*, there are no setae. (Photo credit: Peter Wirtz.)

New Zealand, the North Pacific, etc. Because most larvae settle rapidly, astonishingly dense populations may form, with thousands of individuals per square metre over large areas of suitable substrate, e.g. several endemic rhynchonelliforms on sub-vertical fjord walls in New Zealand, *Terebratulina unguicula* in a similar situation in British Columbia, and *Terebratulina retusa* in Scottish sea-lochs. Very dense, large, deepwater populations of the rhynchonelliform *Laqueus californianus* that were recently discovered along the San Gregorio fault trace (E. Pacific) may be the Recent counterparts of localized Cretaceous populations inferred to have inhabited methane and sulfide cold-seep sites, but chemosymbionts of living brachiopods are not known; seep populations presumably feed on associated chemotolerant or chemosynthetic microorganisms. Brachiopods are not important members of the characteristic fauna of hydrothermal vents associated with mid-ocean spreading ridges. **See also:** Deep ocean ecosystems

Habits and Life Histories

All brachiopods reproduce sexually, generally with separate sexes and approximately equal sex ratios (where known) and a standard haploid gamete/diploid zygote reproductive cycle, but a few may be hermaphroditic. Larvae and adults are diploid, with meiosis producing typical oocytes and sperm. Genomic deoxyribonucleic acid (DNA) content (where known) is among the lowest for metazoans ($c. 4 \times 10^8$ bp per haploid genome), with seven or eight small chromosomes. The ciliated embryos of linguates hatch from small eggs and spend months as juveniles, feeding in the plankton. They are therefore widely distributed; one tiny discinoid (*Pelagodiscus*) is literally cosmopolitan. All other brachiopod larvae (craniate inarticulates and all rhynchonelliforms) develop from larger, yolky eggs and typically settle and metamorphose within a few days of release. In rich environments (e.g. a Scottish sea-loch), spawning is typically annual or biannual, with a *Terebratulina* female of average size releasing about 10 000 eggs from relatively massive gonads. Where food is scarce (e.g. in deep oceanic water), individuals may form mature gametes only rarely. At settlement, larvae are negatively phototropic and able to select suitable substrates. Because their larvae generally settle soon after release, clusters of rhynchonelliforms of successive generations are often found, with younger animals attached to older ones. In genera (e.g. *Neothyris*, *Anakinetica*) that become free living after outgrowing small anchors, the pedicle atrophies and the shell becomes thickened near the hinge, so that the gape is held above the surface sediment. A similar habit was independently acquired by various fossil forms, some of which (e.g. *Gigantoproductus*) were supported by spines rather than differential weighting. **See also:** Meiosis

Feeding is selective (phytoplankton preferred), with oversize or otherwise unwanted particles rejected by local

changes in lophophore ciliary action or flicked away by a tentacle. About two-thirds of particles in the 5–10 μm range may be captured from the flow of $c. 20\text{--}1200\text{ mL water h}^{-1}$ through the mantle cavity. Especially in cold-water environments, brachiopod growth is seasonal, tissue mass being lost in winter. Distinct growth bands are often formed in the shell, and oxygen isotope (O^{18}) composition may be used to provide a high-resolution record of water conditions at the time of shell secretion.

In general, brachiopods are low-energy organisms. Their maximum oxygen demand is low and their minimum demand vanishingly small. Only burrowing linguates are known to employ an oxygen-carrying protein (haemerythrin). Individuals of some genera (e.g. *Terebratulina*) have been kept unfed in seawater aquaria (at 10°C) for as long as a year, after which much tissue had been resorbed but the lophophore still functioned. The persistence of brachiopods since the Early Cambrian may reflect this ability to survive in cold environments with scarce food. Both recent and fossil brachiopod shells occasionally show predator damage and repair, but tissues from living brachiopods are generally repellent to fish and crustaceans, suggesting that chemical defences may also have played some part in their long history.

Fossil History

Brachiopod shells are relatively fragile. Nevertheless brachiopods are among the earliest shelly fossils to appear in Lower Cambrian strata (e.g. the Chengjiang fauna) and are common fossils throughout the Palaeozoic because they were among the dominant filter feeders until the Permian–Triassic mass extinction, when their diversity fell by about two-thirds to a new, fairly stable level (**Figure 6**). When brachiopods were at their peak, before the rise of molluscs and corals, they were among the principal reef builders in shallow seas, but they also explored many other life styles compatible with their structural limitations, including scallop-like jet propulsion. No certain fossil phoronid is known, but the Devonian trace fossil, *Talpina*, is a strong candidate, comparable to extant *Phoronis ovalis*. **See also:** Extinction: End-Permian mass extinction; Post-Permian radiation; Tying in the sea – reefs and burrows (late Palaeozoic)

Phylogeny and Systematics

Metazoan animals are often divided into two categories, protostomes and deuterostomes, according to how the mouth, anus and coelom develop in the early embryo, and the majority of modern zoologists have concluded that brachiopods, phoronids and ectoproct bryozoans fit the deuterostome pattern. Some earlier workers considered brachiopods to be protostomes, although some also recognized a mixture of features and put them in an intermediate

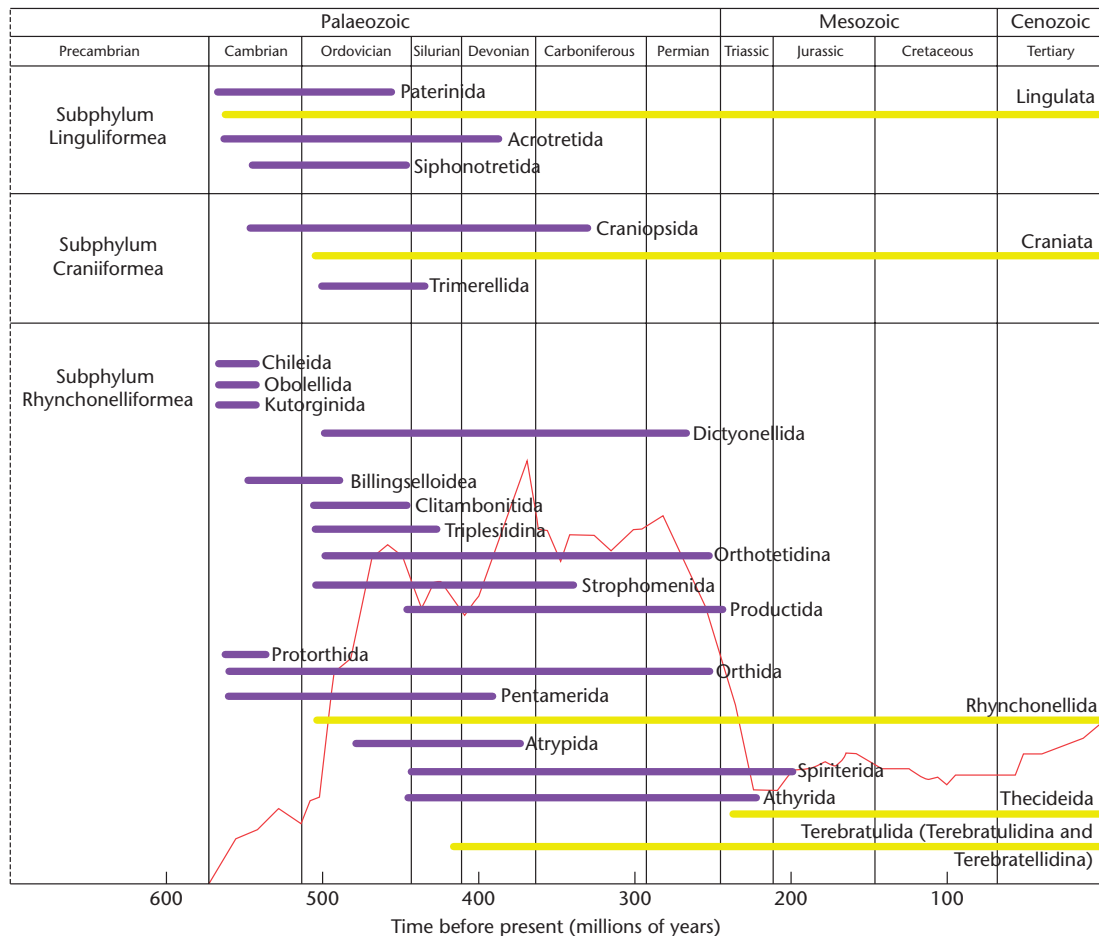


Figure 6 Time ranges of principal brachiopod lineages. (Modified from Williams A, Carlson SJ, Brunton CHC, Holmer L and Popov L (1996) A supra-ordinal classification of Brachiopoda. *Philosophical Transactions of the Royal Society, B* 351: 1171–1193). Lineages surviving to the present day are coloured yellow. The background curve gives an impression of changing family-level diversity through geological time. (After Rudwick, 1970.)

or indeterminate position. Evidence from the comparison of DNA sequences (some from the author's laboratory) shows that brachiopods and phoronids form a clade and convincingly associates them with other undoubted protostomes (e.g. annelids and molluscs) in a supra-phylum alliance, the 'lophotrochozoa' (Figure 7). Thus, the embryological and other morphological characters previously used to define high-level brachiopod relationships are in doubt, either because of unrecognized homoplasy or because they are plesiomorphic, i.e. inherited from the last common ancestor of both protostomes and deuterostomes. It may be more realistic to define these alliances as DNA-based clades, 'Protostomozoa' and 'Deuterostomozoa'. **See also:** Cladistics

As with the origin of all phyla, the origin of brachiopods remains enigmatic. Before the first undoubted brachiopod fossils appear in the Lower Cambrian there existed a quite varied fauna whose mineralized remains are known as 'small shelly fossils', as well as somewhat more

brachiopod-like, but still enigmatic, forms such as *Micrina* and *Mickwitzia*, any of which could represent the form of the stem group from which brachiopods proper were derived. More enigmatic still are slug-like animals such as *Halkieria*, which combined a covering of mineralized sclerites with superficially brachiopod-like anterior and posterior shells. A notable similarity between living brachiopods, annelids and some other lophotrochozoans is provided by the ultrastructure and mode of development of chitinous setae (chaetae), while at least superficial similarities link brachiopod shell punctae and the aesthetes of chiton shells (Mollusca: Polyplacophora). Moreover, some gene trees place chitons very close to brachiopods, perhaps because both have experienced low rates of gene sequence evolution. Presumably these and other such enigmas reflect the sorting out of ancestral morphological characters during the period when stem group metazoans were diverging into the distinct phyla we recognize today. **See also:** Molecular phylogeny reconstruction

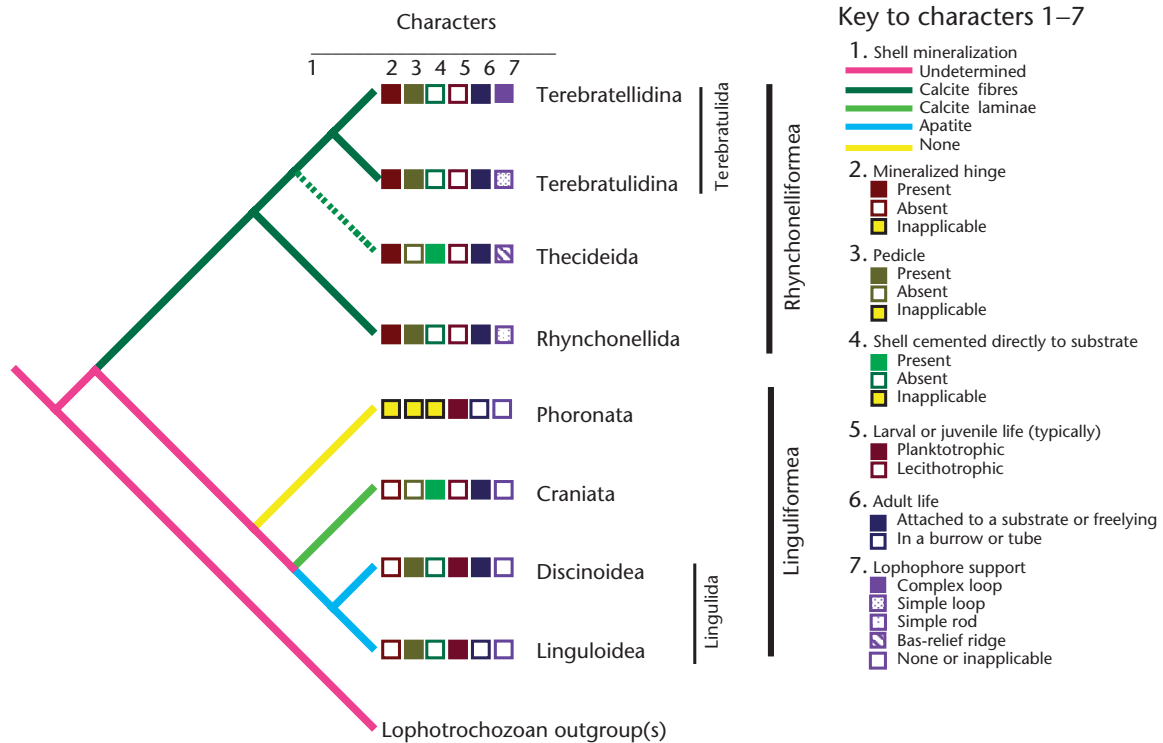


Figure 7 Phylogeny of brachiopods and phoronids, summarizing recent gene sequence evidence and showing the distribution of key characters mentioned in the text. The uncertain placement of the thecideidine lineage within rhynchonelliforms is indicated by a dashed line.

Because ~95% of all ~5000 described brachiopod genera are extinct, most descriptive and taxonomic work, as well as ideas about phylogeny, have been based on the evolution of fossil shell form and (inferred) function. Many details of this brachiopod phylogeny and its expression in Linnean ranks (orders, families, etc.) have been confirmed by recent DNA sequence-based phylogenetics, but DNA-based studies have also led to new insights and to the recently proposed revision of the high-level classification that is followed in this article.

Phylum Brachiopoda (Only extant taxa are listed)

Subphylum Linguliformea

Class Craniata

Order Craniida

Class Lingulata

Order Lingulida

Super-family Linguloidea

Super-family Discinoidea

Class Phoronata

Order Phoronida

Subphylum Rhynchonelliformea

Class Rhynchonellata

Order Thecideida

Order Rhynchonellida

Order Terebratulida

Super-family Terebratulidina

Super-family Terebratellidina

Further Reading

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